Dynamics of Water in Zea Mays L.
Sensitivity Analysis of TROIKA

Jerry R. Lambert, Donald C. Reicosky
MEMBER
ASAE

ABSTRACT

WATER movement from the soil into roots, through the plant, and out into the atmosphere in response to the microclimate was simulated for field-grown maize (sweet corn) plants. Predicted leaf water potentials were compared with field-measured values. A sensitivity analysis of the simulation model was performed to indicate the required measurement accuracy for certain parameters.

Variations in internal plant (stem) resistance and leaf area significantly affected leaf water potential predictions. Root length and root permeability had less dramatic effects. The model is relatively insensitive to changes in root radius and leaf width.

INTRODUCTION

All physiological processes in a crop depend on water status of the organ. Photosynthesis, cell expansion, translocation, etc., are all water-dependent and essential to a healthy, growing and productive crop. Increases in food production efficiency may be possible when we understand more fully the dynamic behavior of water in growing plants.

Water potential gradients cause water to move from the surrounding soil to root surfaces, through the plant and out into the atmosphere. The transport processes are dynamic and the rates are transient. Steady state is seldom the case. Thus the microclimate variables are of prime importance in driving the system. No two crop systems behave alike due to differences in hydraulic characteristics of the soil, variations in rooting behavior, climatic differences, and inherent crop characteristics.

Many research workers have investigated water relations in plants. Considerable emphasis has been placed on evaluating flow and resistances to flow in specific plant parts, e.g., roots (e.g., Busscher and Fritton, 1978; Landsberg and Fowkes, 1978; Meyer et al., 1978; Shalhevet et al., 1976) and the (near) total plant (e.g. Meyer and Ritchie, 1980; Hansen, 1974; Hailey et al., 1973). Several attempts to relate plant and soil resistances have also been made (e.g. Burch, 1979; Ruckenbauer and Richter, 1980; Reicosky and Ritchie, 1976).

Radial flow of water to a single root was used by Philip (1957) and Gardner (1960) to study water movement with emphasis on steady-state soil water. Molz and Remson (1971), Whisler et al. (1968) and Gardner (1964) conducted macroscopic studies of moisture removal from the root zone. They did not consider the effects of roots on the aerial portion of the crop. Nimah and Hanks (1973) developed a macroscopic model to predict water content profiles, evapotranspiration, water flow from or to the water table, root extraction, and root water potential under transient field conditions, but their model does not predict leaf water potentials where many key physiological processes occur. It does provide a "stem" water potential however. Taylor and Klepper (1978) presented a model to predict diurnal soil, root and plant water potentials. This model requires accurate input rates of plant transpiration and root water uptake from each soil layer. Molz (1976) used transient radial flow models to study water movement to plant roots, again without considering the influence of the aerial portion of the crop on the water potential within the soil-plant-atmosphere system. Hillel et al. (1975) and Belmans et al. (1979) used a transient radial flow model that yielded plant water potentials necessary to maintain different uptake rates.

The power of systems analysis is limited when the entire interacting system is not included within the analysis, as in the case when a potential is forced to occur at a specific point in a system—e.g., when a water potential is assumed within the root xylem tissue or at the root-soil interface. Federer (1979) simulated the soil-plant-atmosphere system for forest species to estimate transpiration. Hansen (1975) combined Gardner's model (1960) for water flow to single roots, Monteith's model (1965) of the atmosphere, and internal crop considerations to simulate water transport in a growing crop. Lambert and Penning de Vries (1973) simulated the entire soil-plant-atmosphere system. Though somewhat simplified, the model did not force any potentials or fluxes to be fixed within the system. This paper and its companion (Reicosky and Lambert, 1977) continue the efforts of Lambert and Penning de Vries (1973) to dynamically simulate water movement and potentials throughout the soil-plant-atmosphere systems.
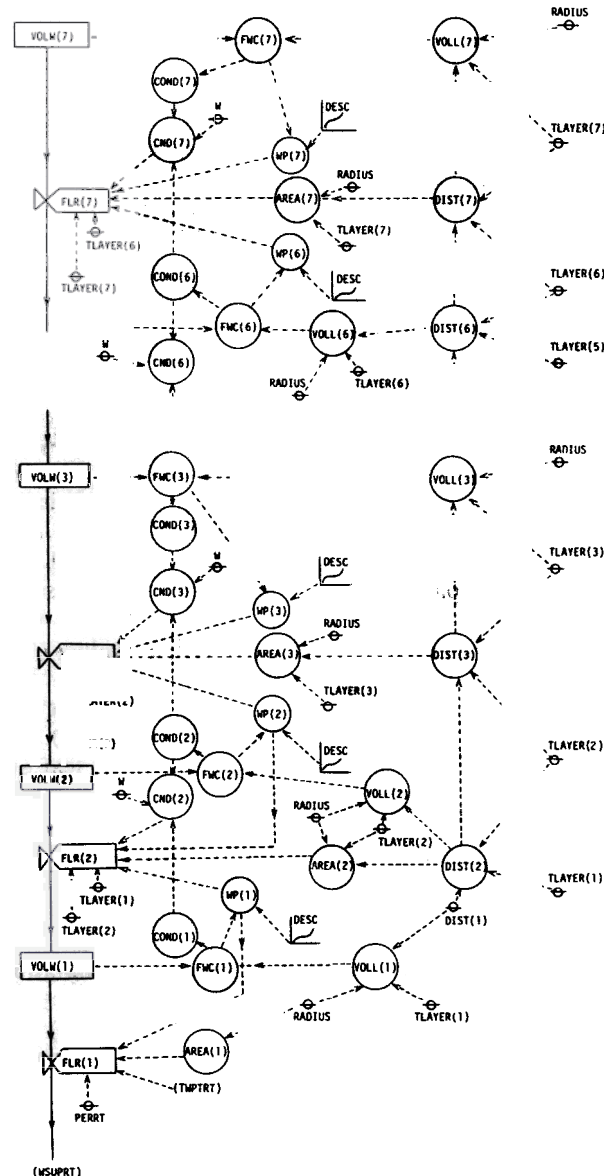
OBJECTIVES

Water movement and potentials directly affect the growth processes of a crop. As we try to optimize the net result of these processes and the associated economics, knowledge of the plant-water status is vital. Therefore, our objective is to quantify the dynamic response of maize to different soil water levels and the environment to determine soil water "treatments" that improve growth and yield. The specific objective of this paper is to perform a sensitivity analysis of six selected plant parameters as they affect leaf water potential simulated

Fig.1 —Schematic representation of the soil-plant-atmosphere system in the model TROIKA.

by the modified model TROIKA to determine the desired observation accuracy of these parameters.

THE MODEL

TROIKA is a model developed by Lambert and Penning de Vries (1971, 1973) to simulate water movement from soil, through the root, stem and leaf system of a bean-like plant which has a single horizontal leaf, and then out into the atmosphere. Although originally developed to describe a bean plant, the model was modified and extended to describe maize. The general model form is schematized in Fig. 1 and outlined below. The specific changes resulting in this version are described.

(a)
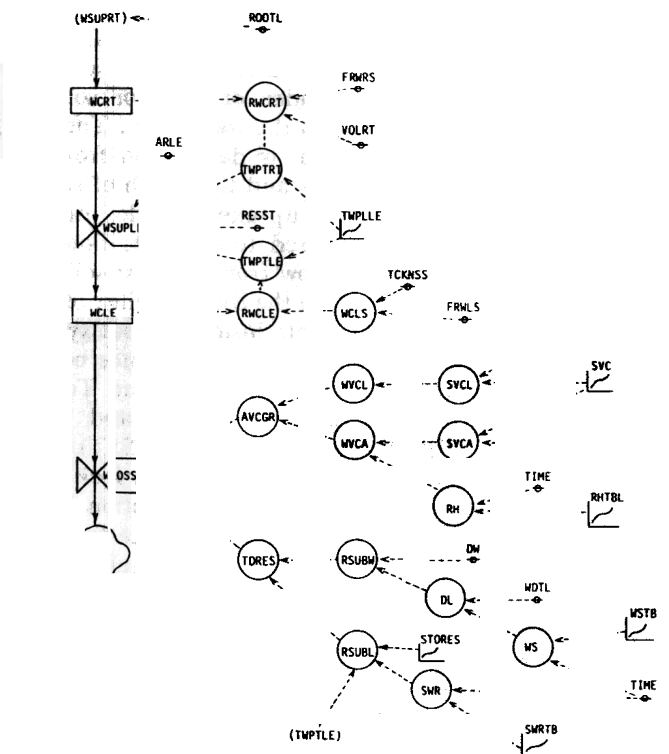
(b)
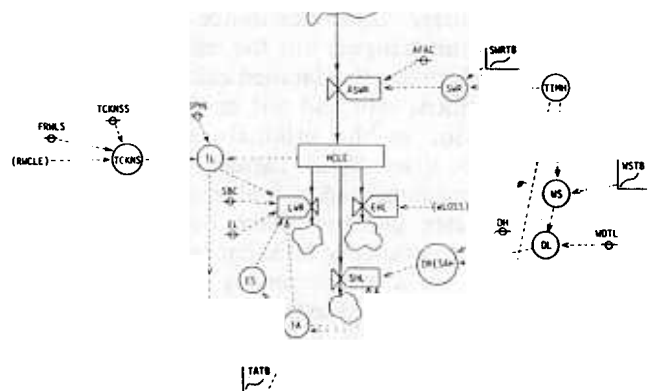
(c)

Fig. 2—System dynamics flow chart of TROIKA. (a) Water flow through soil. (b) Water flow through plant. (c) Heat flow through leaf.

Conceptually, TROIKA is based on a complete but simplified treatment of water movement from the bulk soil, through unsaturated soil to the root surface, through the root and stem to the leaves, and then through the cuticle or stomates and boundary layer into the free atmosphere. Water storage is present in leaves, roots, and in each thin annular cylinder of soil coaxial with the root, and is a level or state variable in system dynamics terminology. Flow between each serial pair of levels depends on the applicable potential difference and the conductivity. Each level is an integral of a net flux rate, which is dependent on system parameters, environmental variables and functional relations as well as potential differences. A continuous, dynamic flow system results.

Water and heat movement in the soil-plant-atmosphere system, as conceptualized in TROIKA, is flow charted in detail in Fig. 2. As indicated schematically by arrows, water moves radially from the outermost annular cylinder or shell of soil through successive shells and into the root xylem. The radius of soil surrounding the root is determined from the soil volume occupied by roots and the length of roots which are active in water uptake. While unsaturated conductivity of soil is used to calculate flow of water between shells of soil, flow from the first soil shell into the root zylem is based on the PERmeability of the RooT (PERRT). Water flow from inside the root xylem to the mesophyll cells is caused by the difference between the Total Water PoTential of the RooT and Total Water PoTential of the LEaves (TWPTRT and TWPTLE) across the RESistance in the STem (RESST) or internal plant resistance, even though we find a lack of data to confirm or disprove this simple assumption. We define stem resistance to be the total resistance from the root xylem to the substomatal cavity. Thus, it includes resistance to flow within the root xylem, in the stem and petiole xylem tissue, and across all tissue between the vein xylem and the substomatal cavity or the epidermal tissue. From the mesophyll tissue water moves into the atmosphere across a combined cuticular resistance and stomatal resistance, hereafter referred to as leaf resistance (RSUBL) in series with the boundary layer resistance (RSUBW).

Determination of the water loss from the leaves has been simplified in this version of the model (Fig. 2b). The boundary layer resistance (RSUBW) remains essentially unchanged, but the leaf resistance (RSUBL) no longer includes the detailed calculations of water and CO_2 movement into and out of the guard cells, which were present in the original version of the model (Penning de Vries, 1972). Instead, experimental data on combined stomatal and cuticular resistance as a function of leaf water potential have been used directly. A maximum resistance of 80 s/cm represents the cuticular resistance, since the stomates are then closed. The stomates are assumed to be closed in darkness and to be as open as allowed by water potential considerations at 0.1 cal/cm²/min radiation. Experimental data were also used to determine leaf water potential from relative water content of the leaf (Reicosky and Lambert, 1977).

The vapor concentration within the substomatal cavity is assumed to be that of saturation, and, therefore, is dependent on leaf temperature. The Initial Leaf Temperature (TLI) is assumed equal to initial (in this study, pre-dawn) air temperature and a dynamic heat balance on the leaves is based on incoming short wave radiation, latent heat of evaporation, convection, reflection and reradiation (Fig. 2c). Long wave radiation from the leaf is calculated using the method of Idso and Jackson (1969).

The concepts were quantified by programming in CSMP (Continuous System Modelling Program) all relationships here described (Lambert and Penning de Vries, 1971).

VALIDATION

Maize (sweet corn) grown at Florence, South Carolina, during 1972 on Varina sandy loam (Reicosky et al., 1975) was used to validate the modified model TROIKA, as reported elsewhere (Reicosky and Lambert, 1977). Certain parameters were obtained from the literature; other parameters and variables were observed experimentally. Initial values of two parameters—PERmeability of the RooT (PERRT) and RESistance of the STem (RESST)—were first estimated from House and Findlay (1966) and Nobel (1974, p. 406), respectively, and then adjusted so that predicted and observed leaf water potentials agreed more closely.

SENSITIVITY ANALYSIS

A sensitivity analysis of a model indicates the response of the predicted variables to variations in the values of the parameters of the model. Thus, we can determine the desired observation accuracy of these parameters.

Six parameters were selected for this sensitivity analysis from about 20 included in the model. Selection of the parameters was based on their strategic position in the flow charts (Figs. 1 and 2) and by intuition. The parameters not included in the sensitivity analysis were either interrelated (e.g. root length, root volume, and number of assumed soil shells); previously investigated (e.g. weighting factor for determining effective conductivity between two adjacent shells (de Wit and van Keulen, 1972); handbook constants (e.g. diffusive coefficient of heat in air); or initial conditions, which could only have an effect during the early times of a simulation (e.g. Initial Leaf Temperature, TLI). The six selected parameters covered those easily observed (leaf width) and those more difficult (stem resistance), average values (root radius) and single values (leaf area), and parameters expected to have the same short-term effect but possibly different long-term effects through feedback (root length and root permeability).

The heat balance is based on exposed leaf area with transpiration from shaded leaves assumed negligible. The actual leaf area per plant is used until the Leaf Area Index (LAI) exceeds 1.0. If a leaf area greater than ground area per plant were used, the incoming radiation intercepted by the plant would exceed the radiation actually available to the plant. Therefore Leaf Area Index is limited to LAI = 1 and is one limitation of the model.

Observed Leaf Water Potential (OLWP) measured with a pressure chamber throughout the day and the predicted Total Water PoTential of the LEaf (TWPTLE) were compared based on:
1. measured average Leaf WiDTh (WDTL),
2. measured LEaf ARea (ARLE), limited to LAI = 1,
3. maize root RADIUS (RADIUS) data from Newman (1973),

**TABLE 1. PARAMETER VALUES USED IN THE MODEL
TO SIMULATE MAIZE LEAF WATER POTENTIAL
ON JULIAN DAY 153.**

Parameter	Units	Irrigated	Non-irrigated
WDTL	cm		
ARLE	cm^2		
RADIUS	mm		
ROOTL	m		
RESST	bar sec/cm^3		
PERRT	cm^3/cm^2 s bar		

4. ROOT Length (ROOTL) calculated from shoot/root ratio data (Reicosky and Lambert, 1977),

5. STem RESistance (RESST) and,

6. RooT PERmeability (PERRT) estimated from House and Findlay (1966) and adjusted to obtain better agreement between predicted and observed leaf water potential.

The base line values of these six parameters are given in Table 1. Julian day 153, 1 June 1972 was chosen for the sensitivity analysis. Observed microclimate data used in the model are shown in Fig. 3 along with the observed and simulated leaf water potentials for the irrigated and non-irrigated treatments described by Reicosky and Lambert (1977).

RESULTS AND DISCUSSION

Both the Observed Leaf Water Potential (OLWP) and that predicted (TWPTLE) using the base line parameters in Table 1 are shown in Figs. 4-13 for comparison. Each parameter is increased and decreased by appropriate multiples of the measured or estimated values so that the effects of variation of the particular parameter can be evaluated.

WiDTh of the Leaf (WDTL) (Fig. 4) is not very significant in predicting leaf water potentials throughout a day in the irrigated treatment. The spread of the curves was even narrower for the non-irrigated treatment (data not shown). The role of leaf width, taken to be the average width of the upper maize leaves, in the model is to determine the thickness of the laminar boundary layer adjacent to the leaf across which water must diffuse to

Fig. 3—Weather data and observed and simulated maize leaf water potentials at Florence, SC on 1 June 1972. Parameters in Table 1 were used as input to the model TROIKA.
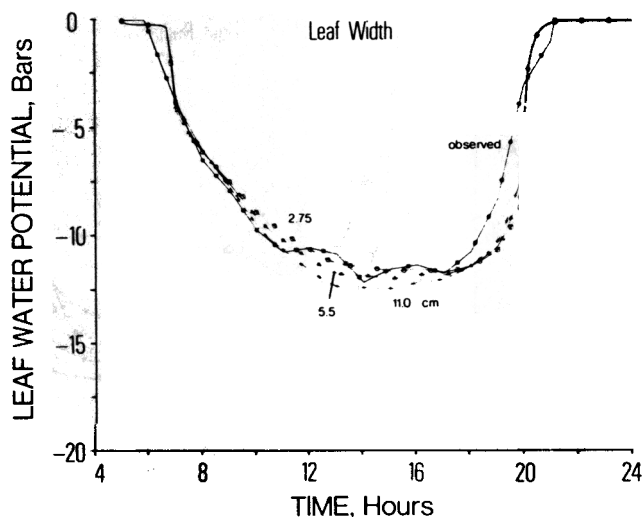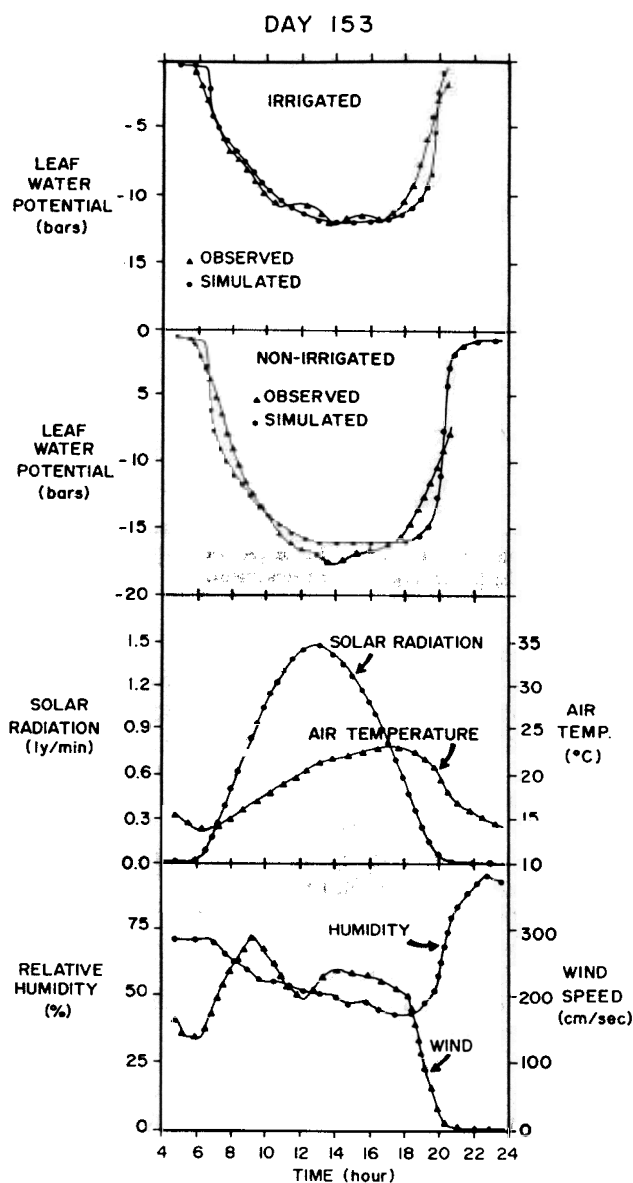

Fig. 4—Comparison of observed leaf water potentials and those predicted by the model TROIKA for three different values of Leaf WiDTh (WDTL) in the irrigated treatment.
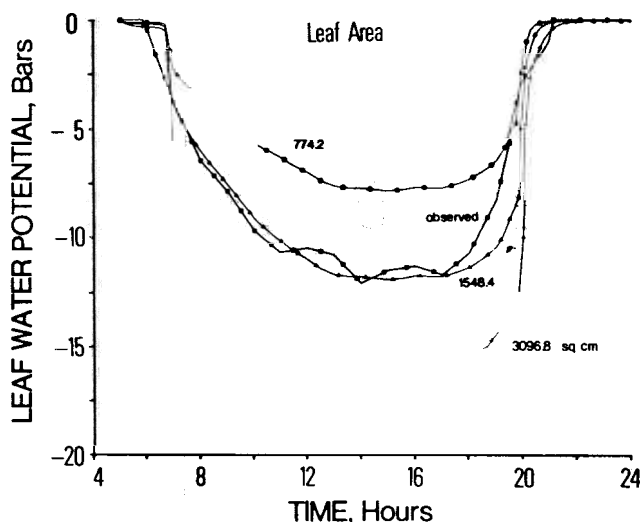

Fig. 5—Comparison of observed leaf water potentials and those predicted by the model TROIKA for three different LEaf AReas (ARLE) in the irrigated treatment.
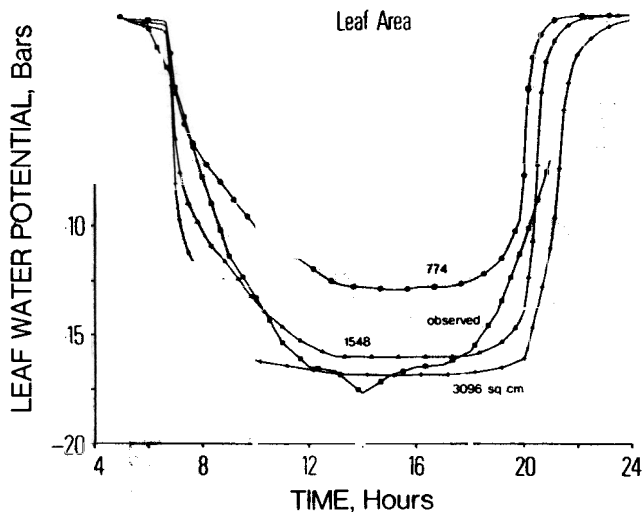
120

Fig. 6—Comparison of observed leaf water potentials and those predicted by the model TROIKA for three different LEaf AReas (ARLE) in the non-irrigated treatment.

Fig. 7—Comparison of observed leaf water potentials and those predicted by the model TROIKA for four different root radii (RADIUS) in the irrigated treatment.

get to the free atmosphere. The equation used is DL = 0.34 WDTL/WS (Monteith, 1965) where DL is the diffusion length and WS is wind speed. The boundary layer resistance is in series with the paralleled stomatal and cuticular resistances. Therefore, as long as the boundary layer resistance is relatively low, the total resistance to water diffusion from within the leaf to the free atmosphere is not significantly affected by a variation in leaf width (this occurs when wind speed is relatively high). The implication is that relatively crude leaf width measurements will suffice for use in TROIKA.

LEaf ARea (ARLE) should be determined with considerable more accuracy than that required for leaf width. As can be seen in Fig. 5, a 4-bar difference resulted from halving or doubling the base line leaf area (1548 cm^2) for the irrigated treatment under the environment used for this sensitivity analysis. On the non-irrigated treatment at lower soil moisture, however, a different pattern occurs, as shown in Fig. 6. Although halving leaf area resulted in a 3- to 4-bar increase in leaf water potential from mid-morning to mid-afternoon, doubling the leaf area did not decrease the predicted leaf water potential nearly as much. The implication is that overestimation of leaf area is not as critical as underestimation in the non-irrigated treatment. Eavis and Taylor (1979) found daily transpiration rates of soybeans to almost double when leaf area was doubled under high soil water content.

Leaf area per plant directly affects the amount of radiation absorbed by the leaves of the plant, most of which is used to evaporate water, creating higher flow rates through the plant. For this analysis, an effective leaf area equal to the ground area of 1548 cm^2/plant was used although irrigated plants had about 4600 cm^2 of leaves/plant and non-irrigated plants had about 2250 cm^2/plant. The assumption is that shaded leaves do not transpire significant amounts of water, since most of the energy used to evaporate water during transpiration comes from radiation.

TROIKA is not very sensitive to root radius per se, as shown in Fig. 7 for the irrigated treatment. In the experimentally significant range, even doubling the radius has little effect on the predicted leaf water potential. Any effect was due to the alteration of root
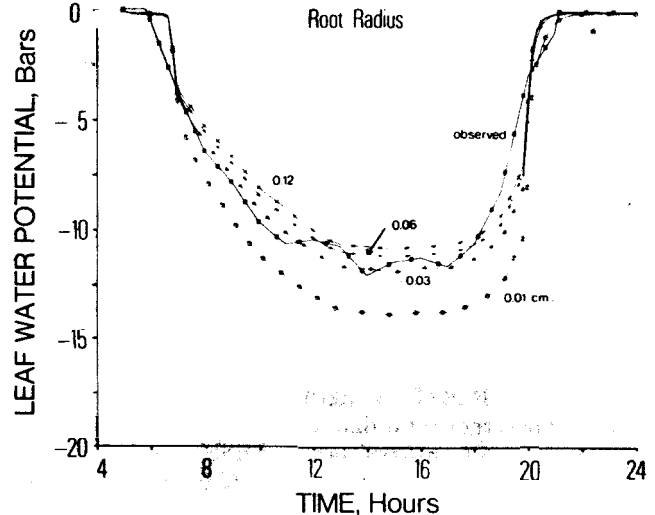
surface area and of the surface areas of the shell interfaces, since the shell thickness does not change.

Convergence of radial flow toward the root changes as root diameter changes. As flowing water converges toward a line sink, velocity increases and potential gradient increases. Thus the larger the root, the less potential drop is necessary.

For the non-irrigated treatment, with dryer soil, variation in the root radius had a different pattern of effect, as in Fig. 8. According to model implications an increase in root radius gives the root access to more water. Thus, for the non-irrigated treatment, where transmission of water in the soil toward the root is more of an impediment than in the irrigated treatment, an increase in root radius from the base line (0.03 cm) results in a relatively higher predicted leaf water potential than for the irrigated treatment. Similarly a decrease to 0.01-cm radius has relatively greater effect for the irrigated treatment because the higher uptake rate causes more effect due to convergence of flow toward the root. The insensitivity of leaf water potential to root radius is corroborated by Williams (1976) who predicted
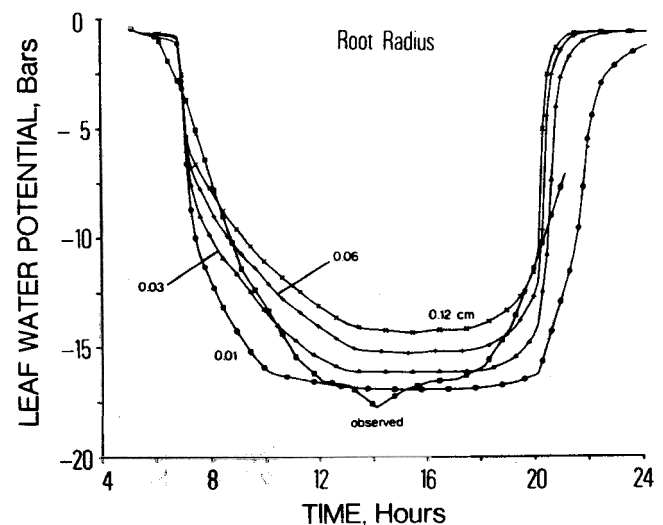

Fig. 8—Comparison of observed leaf water potentials and those predicted by the model TROIKA for four different root radii (RADIUS) in the non-irrigated treatment.
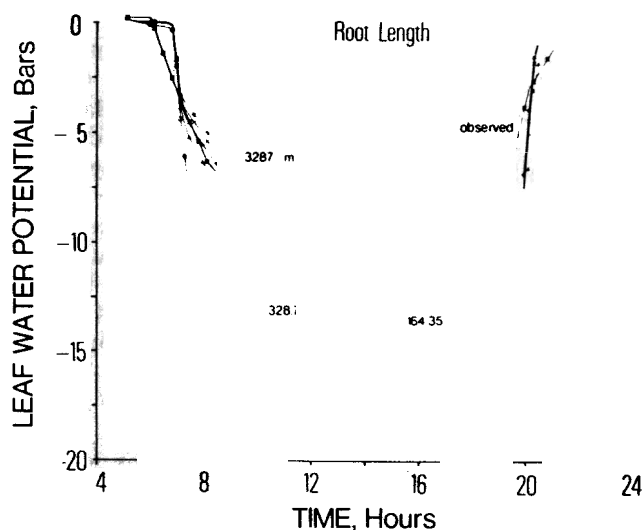
Fig. 9—Comparison of observed leaf water potentials and those predicted by the model TROIKA for five different root lengths (ROOTL) in the irrigated treatment.
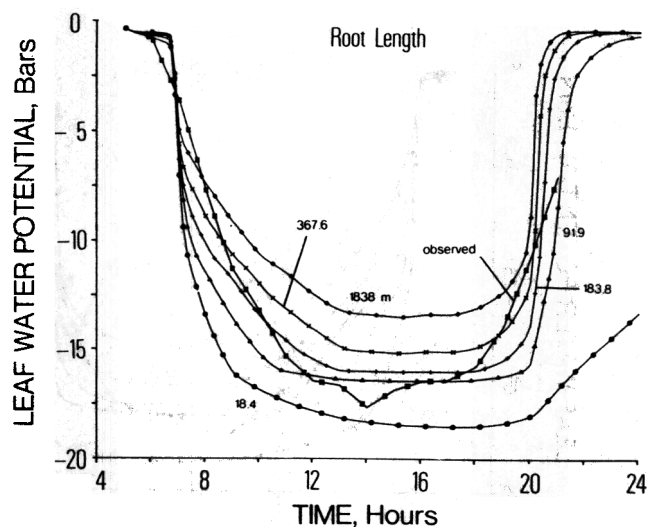

Fig. 10—Comparison of observed leaf water potentials and those predicted by the model TROIKA for five different root lengths (ROOTL) in the non-irrigated treatment.

water potential difference between root and bulk soil using the models of Gardner (1960) and Cowan (1965).

An overestimate of root length caused less error than an underestimate when trying to predict leaf water potentials using TROIKA (Fig. 9) for the irrigated treatment. Only when we used unrealistically low values of root length (32.87 m) did the simulation show a significant effect on leaf water potentials. For dryer soil, however, varying the root length yielded different results, as indicated in Fig. 10. An increased root length significantly increased leaf water potential since water flux was slower in the dryer soil. Thus, an increase in root length results in increased uptake rates and, consequently, increased leaf water potentials. Eavis and Taylor (1979) found root length to have no significant effect on transpiration of soybean. Williams (1976) found lower matric potential differences betwen the root surface and bulk soil under moist conditions than under dry conditions, but did not estimate plant water potentials.

Under the simulated moist conditions the water supplied to the root is sufficient to maintain the leaf

water potential within ±1 bar for a range of -50 to +100% of the base line root length value. This finding is significant from an experimental standpoint. Root lengths are difficult and laborious to obtain. This indicated range will aid in determining experimental procedures necessary to obtain data satisfactory for use in simulation of water flow in the soil-plant-atmosphere system. Caution must be exercised, however, when using dryer soils.

Root permeability (PERRT) effects on simulated leaf water potential shown in Fig. 11 are very similar to those of root length shown in Fig. 9. Since an increase in either parameter causes a linear increase in the rate of water flowing into the root, the similar effects are not contradictory. We expected that the nonlinear conductivity effects of decreased water in the shell, e.g. immediately surrounding a shorter root length, would cause at least slightly different long-term results than a decreased root permeability. Evidently, under the moist conditions used for this analysis, the decreased soil water content near the root had essentially no effect on water flow to the root. The root permeability effects were very
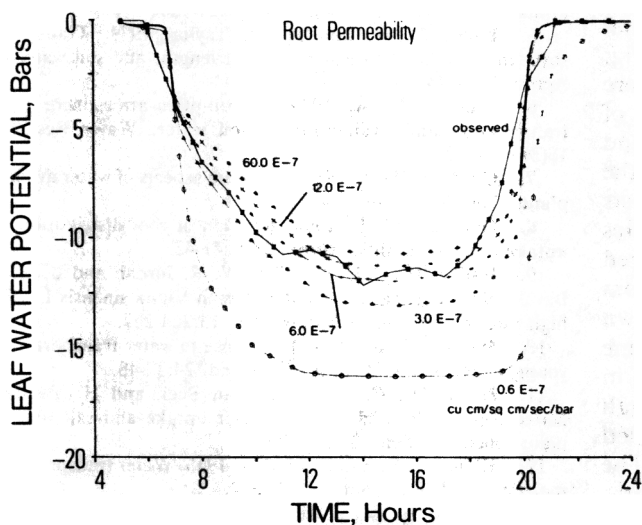

Fig. 11—Comparison of observed leaf water potentials and those predicted by the model TROIKA for five different values of root permeability (PERRT) in the irrigated treatment.
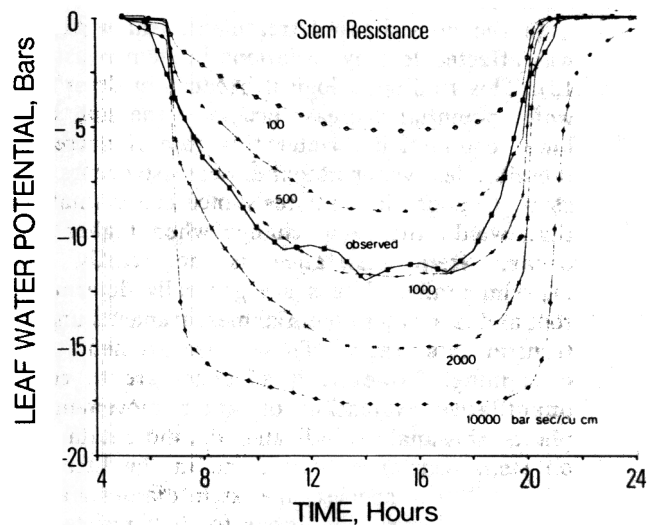

Fig. 12—Comparison of observed leaf water potentials and those predicted by the model TROIKA for five different values of stem resistance (RESST) in the irrigated treatment.
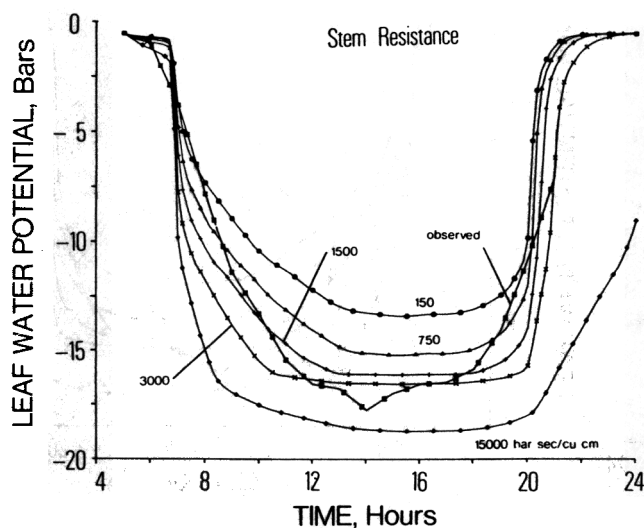
Fig. 13—Comparison of observed leaf water potentials and those predicted by the model TROIKA for five different values of stem resistance (RESST) in the non-irrigated treatment.

similar to root length effects for the non-irrigated treatment (data not shown) also.

Fig. 12 shows the extreme sensitivity of predicted leaf water potential to stem resistance (RESST). While our stem resistance involves some simplifying assumptions, it is similar in concept to the connection resistance arbitrarily defined by Meyer and Ritchie (1980) or to frictional resistance between culm and leaf, found to be of major importance by Ruckenbauer and Richter (1980). Halving or doubling this parameter caused variations of 3 to 4 bars water potential away from the base line leaf water potential. Most of the potential drop occurs within the plant under conditions of moist soil and relatively high transpiration rates (Lambert and Penning de Vries, 1973). This fact is hinted at by results of the sensitivity analysis of root length, pointed out more strongly by results from the stem resistance analysis, indicated by the simulated values of leaf and root water potentials, and supported by the literature (Reicosky and Ritchie, 1976; Newman, 1973; and Molz, 1976). Thus, it should not be surprising that leaf water potential, as calculated by the model, is particularly sensitive to the stem resistance parameter.

In the non-irrigated treatment, leaf water potential was affected less by variations in stem resistance (Fig. 13). This finding is logical because in dryer soil, more water potential decrease occurs in the soil, because of lower conductivity, water flux rate is decreased, and therefore less water potential decrease occurs across the stem. Changes in stem resistance cause smaller effects than would the same change when higher flux rates occur. Stem resistance is not easily measured experimentally. Values are generally determined from root and leaf water potential measurements under known transpiration rates. These measurements are time consuming. However, if advances are to continue in quantitative evaluation of water movement through plants, this analysis indicates that more data are needed on stem resistance than those in the literature. The relationship of species, age, stem diameter and length, and physiological conditions to stem resistance are all important.

The present version of TROIKA assumes constant stem resistance and root permeability over all flow rates

and hydration levels. Considerable literature exists to indicate that plant resistance is variable (Jones, 1978) but an equal volume of literature shows plant resistance to be constant (Hailey et al., 1973). We suspect that small variations may exist due to shrinking and swelling of the hydraulic openings, but that most variations reported are actually due to poor measurement or modeling techniques or to failure to include capacitance effects in the system. Jones (1978), for example, combines soil and plant resistances and capacitances such that changes in soil resistance would be indicated as a variable plant resistance.

SUMMARY

The results of this sensitivity analysis of TROIKA—a model for simulating water flow through soil, into and through the plant and into the atmosphere—indicate stem resistance to be of vital importance in calculating leaf water potential. Leaf area should be determined with an accuracy of 5 to 10% to keep simulated leaf water potentials within a bar of the observed leaf water potential. Root length and root permeability have similar, less dramatic effects. The model is relatively insensitive to changes in root radius and leaf width.

Soil moisture content affects the sensitivity of leaf water potential to variations in all system parameters which we studied. Other environmental variables will also affect the sensitivity of leaf water potentials to variations in the system parameters.

Studies of soil-plant-atmosphere water relations sometimes include exploration of root systems in addition to measurements above ground. This sensitivity analysis indicates that root radius can be roughly estimated and that care should be taken not to underestimate root length (or density), by retrieving all roots.

References

1. Belmans, C., J. Feyen and D. Hillel. 1979. An attempt at experimental validation of macroscopic-scale models of soil moisture extraction by roots. Soil Science 127:174-186.
2. Burch, G. J. 1979. Soil and plant resistances to water absorption by plant root systems. Aust. J. Agric. Res. 30:279-292.
3. Busscher, W. J. and D. D. Fritton. 1978. Simulated flow through the root xylem. Soil Science 125(1):1-6.
4. Cowan, I. R. 1965. Transport of water in the soil-plant-atmosphere system. J. Appl. Ecol. 2:221-239.
5. Eavis, B. W. and H. M. Taylor. 1979. Transpiration of soybeans as related to leaf area, root length, and soil water content. Agron. J. 71:441-445.
6. Federer, C. A. 1979. A soil-plant-atmosphere model for transpiration and availability of soil water. Water Res. Research 15(3):555-562.
7. Gardner, W. R. 1960. Dynamic aspects of water availability to plants. Soil Science 89:63-67.
8. Gardner, W. R. 1964. Relation of root distribution to water uptake and availability. Agron. J. 56:41-45.
9. Hailey, J. L., E. A. Hiler, W. R. Jordan and C. H. M. van Bavel. 1973. Resistance to water flow in Vigna sinensis L. (Endl.) at high rates of transpiration. Crop Sci. 13:264-267.
10. Hansen, G. K. 1974. Resistance to water transport in soil and young wheat plants. Acta Agric. Scand. 24:37-48.
11. Hillel, D., C. G. E. M. van Beek and H. Talpaz. 1975. Microscopic-scale model of soil water uptake and salt movement to plant roots. Soil Sci. 120:385-399.
12. House, C. R. and N. Findlay. 1966. Water transport in isolated maize roots. J. Exp. Bot. 17:344-354.
13. Idso, S. B. and R. D. Jackson. 1969. Thermal radiation from the atmosphere. J. Geoph. Res. 74:5397-5402.
14. Jones, H. G. 1978. Modeling diurnal trends of leaf potential in transpiring wheat. J. Appl. Ecol. 15:613-626.

15. Lambert, J. R. and F. W. T. Penning de Vries. 1971. The Model TROIKA: Listing. Agric. Engr. Res. Ser. No. 16, S.C. Agric. Expt. Sta., Clemson.

16. Lambert, J. R. and F. W. T. Penning de Vries. 1973. Dynamics of Water in the soil-plant-atmosphere system: A Model named TROIKA. pp. 257-273 in Hadas, A. et al., eds. Ecological Studies: Analysis and Synthesis, V. 4. Springer-Verlag, Berlin.

17. Landsberg, J. J. and N. D. Fowkes. 1978. Water movement through plant roots. Ann. Bot. 42:493-508.

18. Meyer, W. S., E. L. Greacen and A. M. Alston. 1978. Resistance to water flow in the seminal roots of wheat. J. Exp. Bot. 29(113):1451-1461.

19. Meyer, W. S. and J. T. Ritchie. 1980. Resistance to water flow in the sorghum plant. Plant Physiol. 65:33-39.

20. Molz, F. J. and I. Remson. 1971. Application of an extraction-term model to the study of moisture flow to plant roots. Agron. J. 63:62-77.

21. Molz, F. J. 1976. Water transport in the soil-root system: Transient analsysis. Water Res. Research 12:805-808.

22. Monteith, J. L. 1965. Evaporation and environment. Symp. Soc. Exp. Biol. 29:205-234.

23. Newman, E. I. 1973. Permeability to water of the roots of five herbaceous species. New Phytol. 72:547-555.

24. Nimah, M. N. and R. J. Hanks. 1973. Model for estimating soil water, plant and atmosphere interrelations. I. Description and sensitivity. SSSA Proc. 37:522-527.

25. Nobel, P. S. 1974. Introduction to Biophysical Plant Physiology. W. H. Freeman & Co., San Francisco.

26. Penning de Vries, F. W. T. 1972. A model for simulating transpiration of leaves with special attention :) stomatal functioning. J. Appl. Ecol. 9:57-77.

27. Philip, J. R. 1957. The physical principles of water movement during the irrigation cycle. Proc. 3rd. Int. Cong. Irrig. Drainage 8:125-128.

28. Reicosky, D. C., R. B. Campbell and C. W. Doty. 1975. Diurnal fluctuation of leaf-water potential of corn as influenced by soil matric potential and microclimate. Agron. J. 67:380-385.

29. Reicosky, D. C. and J. R. Lambert. 1977. Dynamics of water in the soil-plant-atmosphere system: Comparison of field measured and simulated corn leaf water potential. SSSAJ 42:221-228.

30. Reicosky, D. C. and J. T. Ritchie. 1976. Relative importance of soil resistance and plant resistance in root water absorption. SSSAJ 40:293-297.

31. Ruckenbauer, P. and H. Richter. 1980. Frictional resistances to water transport in water-cultured wheat plants. Phyton 20:37-45.

32. Shalhevet, J., E. V. Maas, G. J. Hoffman and G. Ogata. 1976. Salinity and the hydraulic conductance of roots. Physiol. Plant. 38:224-232.

33. Taylor, H. M. and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. Adv. Agron. 30:99-128.

34. Whisler, F. D., A. Klute and R. J. Millington. 1968. Analysis of steady state evapotranspiration from a soil column. SSSAJ 32:167-174.

35. Williams, J. 1976. Dependence of root water potential on root radius and density. J. Exp. Bot. 27(96):121-124.

APPENDIX
DICTIONARY OF VARIABLES

AFAC	Absorption factor for short wave radiation, dimensionless
AREA(I)	Area of inner surface of i'ᴬ soil shell, cm²/cm root
ARLE	Area of leaves, cm²
ASWR	Absorbed short wave radiation, cal/cm²min
AVCGR	Actual vapor concentration differential, g/m³
CND(I)	Average conductivity of soil shells i and i-1, cm/min
COND(I)	Conductivity of i'ᴬ soil shell, cm/min
DESC	Desorption curve for Varina sandy loam, water content vs soil water matric potential
DH	Diffusive constant for heat in air, cm²/s
DIST(I)	Distance from root surface to center of i'ᴬ soil shell, cm
DL	Diffusive length of boundary layer, cm
DRESAH	Diffusive resistance of boundary layer to heat, s/cm
DW	Diffusive constant for water, cm²/s
EHL	Evaporative heat loss, cal/cm²min
EL	Emissivity of leaf, dimensionless
ES	Emissivity of sky, dimensionless
FLR(I)	Flow rate of water from the i'ᴬ soil shell, cm³/min cm root
FRWLS	Fraction of water in leaf when saturated, dimensionless
FRWRS	Fraction of water in root when saturated, dimensionless
FWC(I)	Fractional water content of i'ᴬ soil shell, cm³/cm³
HCLE	Heat content of leaves, cal/cm²
LWR	Long wave radiation from the leaf, cal/cm²/min
OLWP	Observed leaf water potential, bars
PERRT	Permeability of root, cm³/cm² s bar. Defined to be between the root surface and the root xylem
RADIUS	Effective radius of root, cm
RESST	Stem resistance, bar s/cm³. Defined to be between root xylem and leaf mesophyll tissue
RH	Relative humidity of free atmosphere, %
RHTBL	Table of relative humidity by time of day
ROOTL	Root length, cm
RSUBL	Diffusive resistance of stomates and cuticle to water, s/cm
RSUBW	Diffusive resistance of boundary layer to water, s/cm
RWCLE	Relative water content of leaves, %
RWCRT	Relative water content of root, %
SBC	Stefan-Boltzmann constant cal/cm² °C⁴ min
SHL	Sensible heat loss, cal/cm² min
SPHL	Specific heat of leaf, cal/cm³ °C
STORES	RSUBL vs leaf water potential function
SVC	Saturation vapor concentration vs temperature function
SVCA	Saturation vapor concentration of atmosphere, g/m³
SVCL	Saturation vapor concentration of leaves, g/m³
SWR	Incoming short wave radiation, cal/cm² min
SWRTB	Table of SWR by time of day
TA	Temperature of air, °C
TATB	Table of air temperature by time of day
TCKNS	Thickness of leaf, cm
TCKNSS	Thickness of leaf when saturated, cm
TDRES	Total diffusion resistance between substomatal cavity and free atmosphere, s/cm
TIMH	Time, h
TL	Temperature of leaf, °C
TLI	Initial leaf temperature, °C
TLAYER(I)	Thickness of i'ᴬ soil shell, cm
TWPLLE	Leaf water potential vs relative water content function
TWPTLE	Total water potential of leaves, bars
TWPTRT	Total water potential of root, bars
VOLL(I)	Volume of i'ᴬ soil shell, cm³/cm root
VOLRT	Volume of root, cm³
VOLW(I)	Volume of water in the i'ᴬ shell of soil, cm³/cm root
W	Weighting factor for averaging conductivity of adjacent soil shells, dimensionless
WCLE	Water content of leaves, mg/cm²
WCLS	Water content of leaves when saturated, mg/cm²
WCRT	Water content of root, mg
WDTL	Width of leaf, cm
WLOSS	Rate of water loss from leaves, mg/cm² min
WP(I)	Water potential of i'ᴬ soil shell, bars
WS	Wind speed, cm/s
WSTB	Table of wind speed by time of day
WSUPLE	Water supplied to leaves, mg/min
WSUPRT	Water supplied to the total root, mg/min
WVCA	Water vapor concentration of atmosphere, g/m³
WVCL	Water vapor concentration of leaf, g/m³